Auditory sensitivity in aquatic animalsa)

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FORUM

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Auditory sensitivity in aquatic animals[a)]

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A critical concern with respect to marine animal acoustics is the issue of hearing "sensitivity," as it is widely used as a criterion for the onset of noise-induced effects. Important aspects of research on sensitivity to sound by marine animals include: uncertainties regarding how well these species detect and respond to different sounds; the masking effects of man-made sounds on the detection of biologically important sounds; the question how internal state, motivation, context, and previous experience affect their behavioral responses; and the long-term and cumulative effects of sound exposure. If we are to better understand the sensitivity of marine animals to sound we must concentrate research on these questions. In order to assess population level and ecological community impacts new approaches can possibly be adopted from other disciplines and applied to marine fauna.

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I. INTRODUCTION

Research on the bioacoustics of marine animals has been conducted for over a century and has intensified over the past decades. This increase in research is closely tied to growing awareness of the potential effects of anthropogenic (man-made) noise[1] on aquatic animals (National Research Council, 2005; Nowacek *et al.*, 2007; European Commission, 2008; Clark *et al.*, 2009; Schipper *et al.*, 2008; Williams *et al.*, 2014). Despite substantial progress, however, major aspects of marine animal bioacoustics remain unresolved and science is still far from providing a comprehensive assessment of the potential for noise-induced effects on marine fauna (Southall *et al.*, 2007; Popper *et al.*, 2014; Hawkins *et al.*, 2014; Popper and Hawkins, 2016). One of the most critical concerns with regards to bioacoustics is the issue of hearing "sensitivity," as it is widely used as criterion for the onset of noise-induced effects. The objectives of this forum letter are to (i) define auditory sensitivity to sound, (ii) address uncertainties when examining the acoustic sensitivities of aquatic animals, (iii) briefly discuss long-term consequences to hearing of sound exposure, and (iv) highlight a potential alternative approach to assessing sensitivity to sound, taking into account population based effects of underwater sound.

II. SENSITIVITY

In audiometry, the term sensitivity generally refers to auditory perception or the physiological response(s) of an individual, or group of individual's, to sound. This may include the effects of noise upon animals in terms of changes in hearing sensitivity due to temporary or permanent damage to sensory cells of the ear, or (when referring to behavioral sensitivity) any behavioral disturbance it might cause to animals. The threshold for onset of behavioral disturbance is not to be confused with the auditory threshold (or hearing threshold) which only reflects how well an animal detects the sound and not the level of sound to which an animal may respond. The hearing threshold is defined herein as the stimulus level corresponding to a 50% correct detection probability (Reichmuth *et al.*, 2013). It is important to specify, however, whether the threshold was determined under quiet conditions or in the presence of other sounds since such sounds can raise thresholds (Yost, 2013).

Any threshold values or sound exposure criteria may specify those sound levels above which particular responses (such as behavioral disturbance or damage to the auditory system) may take place. The assessment end points are typically aimed at determining whether there is a significant impact on populations and on the wider ecosystem.

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III. UNCERTAINTIES

Over a century of auditory research on marine animals has produced audiograms for more than 30 (of 129, Perrin *et al.*, 2009) species of marine mammals and just over 100 of over 32 100 fish species (Fay, 1988; Ladich and Fay, 2013). Only a few species of invertebrates, the most diverse of the three major marine taxa, have been tested for their sensitivity to sound and far more work needs to be done to get a real understanding of sound detection by invertebrates (Budelmann 1992a,b; Samson *et al.*, 2014).

For marine mammals, the challenges of conducting (auditory) research and maintaining animals in research facilities has often resulted in species-defining audiograms being based on a few (or even one) individuals of a species (Kastelein *et al.*, 2010; Pacini *et al.*, 2011). Generalizations on the sensitivities of marine mammals are being based on results from just a few species (National Research Council, 2005; Southall *et al.*, 2007). This has resulted in a very limited understanding of species auditory diversity or variation within species. For those marine mammal species for which we have audiograms from several individuals, such as the bottlenose dolphin (*Tursiops truncatus*), the published auditory thresholds at any one frequency may vary by more than 80 dB between animals (Finneran and Houser, 2006) although wild populations of belugas (*Delphinapterus leucas*) have shown much less variation (Castellote *et al.*, 2014). To some extent this variation may reflect individual differences in such factors as age related effects (Houser and Finneran, 2006) or prior noise exposure histories and can also be influenced by the method for threshold determination (Finneran, 2008).

Similar differences in thresholds have been found in the most widely studied fish species, the goldfish (*Carassius auratus*), and such variation would likely be found in many other fish species where there have been multiple studies (Ladich and Fay, 2013; Sisneros *et al.*, 2016). This variation is largely considered to be a result of the experimental environment, the acoustics of the environment, and/or basic methodology of determining "thresholds" (Popper and Fay, 2011; Rogers *et al.*, 2016). Although there may be differences related to age and size, these remain to be demonstrated.

In invertebrates, thresholds for the detection of underwater sound are too few to make any generalizations or to reach any conclusions. With sound-detection organs varying widely amongst invertebrate species (Budelmann 1992a,b; Popper *et al.*, 2003), it is likely that sensitivities may differ substantially between species, as they do for marine mammals and fishes.

Hearing thresholds and overall sensitivities to sound for the majority of marine species have yet to be defined, leaving great uncertainty regarding how well these species detect and respond to sound. The uncertainty regarding hearing thresholds resulting from this paucity of data is an important limitation in considering the effects of underwater sound. While testing all species is completely unrealistic and unnecessary, the existing information deficit leaves open questions such as: how representative are results obtained from a small number of specimens within a species and what are the influences of size, age, season, motivation, etc., in these results; to what extent can results from one species be transferred or extrapolated to other species within the same taxonomic group; and are there consistent trends/guidelines useable across taxonomic groups?

These questions present substantial challenges for scientists, regulators, and other stakeholders as they seek to manage the uncertainty resulting from species for which we have few data, and for which sensitivity may vary at different life stages. As an example, audiograms of many individual bottlenose dolphins have been measured (Houser and Finneran, 2006; Houser *et al.*, 2008). While much has been gained from these studies, these results are not necessarily representative for other species of toothed whales (Nachtigall *et al.*, 2008; Castellote *et al.*, 2014). Moreover, such data provides no information that relates to baleen whales (National Research Council, 2005; Finneran and Jenkins, 2012).

General functional criteria are often used to characterize hearing sensitivity in different taxonomic groups. Traditional auditory groupings of marine mammals have been based upon the frequency range of their auditory and vocal systems (Ketten, 2000; Southall *et al.*, 2007). In fishes, species have been grouped based upon the presence or absence of hearing specializations and not necessarily on taxonomic relationships. Such specializations include the presence or absence of a swim bladder or other air bubble and its degree of connection to the inner ear (Popper *et al.*, 2014). There are no similar functional auditory criteria yet available for invertebrates, and there are probably far too few data on these species to even consider setting such criteria at this point in time.

Real life hearing thresholds are often ambient noise limited and not sensitivity limited (Hawkins and Chapman, 1975; Dooling and Blumenrath, 2014). Therefore, it is important to monitor ambient noise conditions when auditory thresholds are being determined. Masking studies using tonal sound may not provide a complete description of masking (Kidd *et al.*, 2008; Clark *et al.*, 2009; Fay, 2010; Erbe *et al.*, 2016) as real-life signals are usually not sinusoidal and masking noise may not be Gaussian (Branstetter and Finneran, 2008; Erbe, 2008; Trickey *et al.*, 2011; Branstetter *et al.*, 2013). Sound in the wild is much more complex, and effects such as co-modulation, spatial, or temporal masking release can even lead to a reduction in hearing thresholds (Branstetter and Finneran, 2008). When considering sound detection, a variety of factors creating release from masking need to be considered as well as do the critical ratio and critical bandwidth (Johnson, 1968; Johnson *et al.*, 1989; Kastelein *et al.*, 2009; Turnbull and Terhune, 1990; Southall *et al.*, 2003; see Erbe *et al.*, 2016 for review). More complex studies are needed in order to assess the audibility of a sound by marine animals in their environment, using naturally occurring types of masking sound (Yost, 2013). In this context it is essential to tie masking back to hearing abilities of the animal; referring to masking effects of any sound without reference to hearing would ignore an important aspect and could be misleading. Masking, especially of biologically relevant sound signals involved in communication and orientation, is often overlooked in regulation of underwater noise.

Key objectives of future studies with aquatic animals should include:

- What is the potential of masking from repetitive man-made sounds (e.g., pile driving or seismic surveys) and from continuous man-made sounds (e.g., shipping, gas and oil platforms, underwater renewable energy devices)?
- What are the relative masking effects of the different characteristics of man-made sound compared to that from white noise (the default type of noise used in masking experiments)?
- Which acoustic cues are available and used by a species and which of these cues are masked if the noise level is increased?

In considering behavioral responses, as well as in considering hearing capabilities, it is also important to take account of contextual factors, including location, time of day, time of year, age of the animal, (and more) and their previous experience of sound exposure (Ellison *et al.*, 2011). Behavioral responses of individual animals often depend on their internal state (e.g., hormone levels, general health), motivation (e.g., whether animal is feeding, in reproductive mode, interacting with young), and learned associations between sounds and external information. Animals can learn to exploit sound information and it can result in altering the animals' behavior in response to sound, such as through attraction to a food source (Stansbury *et al.*, 2014). All of these factors affect whether a particular sound will have a deterrent, attractive, or neutral effect on animal behavior. Such considerations should be taken into account for all taxonomic groups. However, this tends to provide an exceedingly high number of variables, many of which are often difficult to quantify.

It is especially important to specify which acoustic characteristics of a stimulus are biologically important for an animal and determine the response of the animal to those characteristics (e.g., frequency, roughness, rise-time, pulse rate). Experiments are needed with sounds that differ in their acoustic characteristics to determine to which features of stimuli animals are most responsive. Much can be learned in this regard from research on terrestrial animals (e.g., on amphibians and birds)—we need to learn from research in other environments (Sun and Narins, 2005; Slabbekoorn *et al.*, 2010; Partan, 2013).

IV. STUDY DESIGN

"A man in the night, who is on his hands and knees searching in the grass under the light of a lamp post. Along comes a second man who asks what the first man is searching for. 'I lost my car keys and I am looking for them,' the first man replies. The second offers to help him look, and after a half an hour of intensive but futile search, he asks, 'Are you sure you lost your car keys here?' 'No, I know I did not lose them here. I lost them about one hundred feet down the road,' replies

the first. 'Then why are you looking for your keys here?' asks the second. To which the first replies, 'Why, there is a lighted lamp post here.'"

[from Harris in discussion of Parvulescu (1967)].

When designing a new research experiment, a key question is always: "Are we asking the right questions or are we doing an experiment merely because it can be done"? The answer to this question clearly depends on the aspect/research question that needs to be addressed. For example, a noise impact experiment investigating the schooling behavior of fishes in response to noise (e.g., Hawkins *et al.*, 2014) may have immediate implications for fisheries, but the results may also be important with regard to the conservation of fish populations. An important aspect of such experiments is, once again, to carry them out under appropriate acoustic conditions with appropriate measurements and metrics employed to describe the received sound stimuli in order to achieve useful results.

Ideally, experiments should be conducted under acoustic conditions reflecting the acoustic conditions experienced by the animals under free-field conditions (Hawkins *et al.*, 2014; Rogers *et al.*, 2016). This is especially important with regards to experiments involving fishes and probably other taxonomic groups that are sensitive to the particle motion component of sound and not always to sound pressure. If we do not monitor and control the appropriate components of sound for a particular species, the results can be misleading (Mooney *et al.*, 2010; for further discussion, see also Popper and Fay, 2011; Popper *et al.*, 2014; Hawkins *et al.*, 2015). When measuring behavioral responses observed from captive marine animals held in a tank it is important to realize that they do not necessarily reflect the full range of natural responses in the wild and conclusions should not be extrapolated to other contexts (Popper *et al.*, 2014; Hawkins *et al.*, 2015).

V. HOW TO DEAL WITH LONG-TERM CONSEQUENCES?

Marine animals live in an environment in which acoustic conditions can vary substantially (Ellison *et al.*, 2011; Erbe *et al.*, 2015). Like terrestrial animals, marine animals have adapted to living in aquatic soundscapes and evolved to deal with their respective levels of background sound (Tyack, 2008). The exact effects of sound on stress levels and the overall health of marine animals, and associated effects on vital functions (e.g., feeding, growth, survival, movements, fecundity) are not well known (Atkinson *et al.*, 2015). The exposure to increasing underwater noise levels due to man-made activities is clearly an issue of concern, but at the moment how an increase in chronic background sound (rather than acute exposure to a particular activity) may affect aquatic animals is unknown. It is also evident that underwater sound and its effect on the marine fauna should not be assessed in isolation, but together with other stressors in the marine environment.

We know that animals may habituate to sounds that are presented repeatedly (Nowacek *et al.*, 2007; Samson *et al.*, 2014), but very few experiments have assessed the significance of repeated exposure in the field. Recovery time following sound exposure is also important, and particularly how the effects accumulate from repeated exposures over time (cumulative exposure). Other issues are of considerable importance such as how effects accumulate with different time intervals between exposures. In addition, the level of adaptation of individuals and their developmental history is important with regards to their auditory system (some more resilient to sound exposure than others).

VI. FUTURE DIRECTIONS

Looking ahead leaves the question: "How do we avoid being at the same level of understanding two decades from now?" There is still a paucity of data for all taxonomic groups with regard to hearing sensitivity, behavioral responses to sound, and ecological effects of sound exposure (such as population level effects or effects on predator-prey interactions). In order to address the significance of behavior it is necessary to assess the importance of any observed changes in behavior as a result of sound exposure. How does the observed behavior affect vital functions and what will that mean in terms of changes to populations? The currently popular approaches to address population effects within a risk assessment framework (PCAD and PCoD)[2] are data hungry and can seldom be applied successfully to marine mammal, fish, or invertebrate species of concern (National Research Council, 2005; Keith, 2008; Muir *et al.*, 2010; Cato *et al.*, 2013). Alternatively, individual-based models are used to predict what an animal might do when it is exposed to sound, but again the results are not widely applicable (Reuter *et al.*, 2011).

Looking at fisheries science, Productivity/Susceptibility Analysis (PSA) (e.g., Patrick *et al.*, 2010) provides a way of assessing the risks to different species based on their life history characteristics. Productivity refers to the number of offspring produced. In general, there are two different evolutionary strategies: *r*-selection (animals producing many offspring, each with a poor chance of survival under natural conditions, e.g., Atlantic cod *Gadus morhua*) vs *k*-selection (animals producing fewer offspring with a higher probability of surviving under natural conditions, e.g., catshark *Scyliorhinus sp*.). In Atlantic cod, mortality is generally enormous and results in only a small number of adults surviving out of millions of eggs. In contrast, catsharks produce only a few offspring that must show high survival. Susceptibility refers to the degree to which sound exposure can have an impact upon a stock or species. Fish species may show extreme differences in their susceptibility to (acoustic) disturbance. Overall, PSA can be used to compare the relative vulnerability of different stocks and species to sound exposure and appropriate mitigation procedures can then be considered.

A comparison of the responses of wild fishes to impulsive sounds (Hawkins *et al.*, 2014) is a good example in this context. European sprat (*Sprattus sprattus*) was compared with Atlantic mackerel (*Scomber scombrus*) at a particular location. For the Atlantic mackerel, as an *r*-strategist, the number of animals that can be extracted from the stocks in general without doing any harm to the overall population is high (except when stocks are overexploited) and the Atlantic mackerel rates low in terms of risk assessment. Sprat laid numerous eggs as well, but in a particular place and time of the year and fewer than the Atlantic mackerel. Also it appears that European sprat may communicate using sound. Their susceptibility to sound exposure is perhaps higher than that of Atlantic mackerel and their vulnerability to sound exposure is probably greater. The European sprat would fit into an intermediate category with respect to risk from sound exposure. If we look at another species living at the same location, the red-mouthed goby (*Gobius cruentatus*) lives on the sea-bed, forms small populations, is a sound-producer, and as a *k*-strategist lays a small number of eggs. It has little resilience in general and it is likely to be exposed to a much greater risk from sound exposure.

The PSA approach has been used in an ecosystem context for managing fisheries. Policies in Europe are now moving toward a multi-species approach in managing fisheries, as different species interact with one another within the ecosystem. It is necessary to consider whether (sound induced) impact on prey also has an effect on the predators and vice versa. In complex systems, single species and single stressor studies (i.e., noise alone) do not necessarily predict the responses of multispecies systems or multistressor assays, both in trophic functioning and the timescales of responses (Pfister *et al.*, 2014). Research on environmental change in the ocean will likely reveal community or systems level impacts and research programs addressing noise should be prepared to detect such changes. With reference to the findings by Hawkins *et al.* (2014), when the European sprat schools break up and individual fish disperse following noise exposure, does that make them more susceptible to predation from Atlantic mackerel? Also, when looking at the ecosystem as a whole, the species at risk may be the least expected ones. The most vulnerable species are not necessarily those that are commercially most valuable. It can be argued that we need to prioritize species according to the role they play within the ecosystem—some are more important in terms of ecosystem integrity than others.

VII. CONCLUSIONS

A number of important research aspects emerge which are relevant for research on sensitivity of sound on marine animals:

- How do we deal with the uncertainty regarding how well these species detect and respond to sound?

- What are the masking effects of man-made sounds on the detection of biologically important sounds by marine animals?
- How do internal state, motivation, context, and previous experience affect behavioral responses and how might these be taken into account?
- How should long-term and cumulative effects be taken into account in assessing the effect of underwater sound on marine animals?
- Can we adopt approaches from other disciplines to assess population level impacts which are then applicable to marine fauna?

These aspects have to become a focus of research if we want to better understand the sensitivity on marine animals for sound and subsequently the effects of underwater sound on these animals. This list is not exclusive, but answering these research questions will provide essential information for a scientifically more meaningful assessment of this issue.

[1]For purposes of this paper, "The term 'noise' is [...] used to describe undesired sound, or sound that interferes with detection of any sound that is of interest" (Popper *et al.*, 2014), or can lead to physical effects. In this paper "the term 'sound' is used both to refer to identifiable man-made sources such as individual ships or oil and gas platforms, or to distant man-made sources that cannot be located or identified" (Popper *et al.*, 2014).

[2]PCAD: Population Consequences of Acoustic Disturbance (National Research Council, 2005); PCoD: Population Consequences of Disturbance (see King *et al.*, 2015).

Atkinson, S., Crocker, D., Houser, D., and Mashburn, K. (**2015**). "Stress physiology in marine mammals: How well do they fit the terrestrial model?," J. Comp. Physiol. B **185**, 463–486.

Branstetter, B. K., and Finneran, J. J. (**2008**). "Comodulation masking release in bottlenose dolphins (*Tursiops truncatus*)," J. Acoust. Soc. Am. **124**, 625–633.

Branstetter, B. K., Trickey, J. S., Bakhtiari, K., Black, A., Aihara, H., and Finneran, J. J. (**2013**). "Auditory masking patterns in bottlenose dolphins (*Tursiops truncatus*) with natural, anthropogenic, and synthesized noise," J. Acoust. Soc. Am. **133**, 1811–1818.

Budelmann, B. U. (**1992a**). "Hearing in crustacea," in *The Evolutionary Biology of Hearing*, edited by D. B. Webster, R. R. Fay, and A. N. Popper (Springer-Verlag, New York), pp. 131–140.

Budelmann, B. U. (**1992b**). "Hearing in non-arthropod invertebrates," in *The Evolutionary Biology of Hearing*, edited by D. B. Webster, R. R. Fay, and A. N. Popper (Springer-Verlag, New York), pp. 141–155.

Castellote, M., Mooney, T. A., Quakenbush, L., Hobbs, R., Goertz, C., and Gaglione, E. (**2014**). "Baseline hearing abilities and variability in wild beluga whales (*Delphinapterus leucas*)," J. Exp. Biol. **217**, 1682–1691.

Cato, D. H., Noad, M. J., Dunlop, R. A., McCauley, R., Gales, N. J., Salgado Kent, C. P., Kniest, H., Paton, D., Jenner, K. C. S., Noad, J., Maggi, A. M., Parnum, I. M., and Duncan, A. J. (**2013**). "A study of the behavioural response of whales to the noise of seismic air guns: Design, methods and progress," Acoust. Aust. **41**, 88–97.

Clark, C. W., Ellison, W. T., Southall, B. L., Hatch, L., Van Parijs, S. M., Frankel, A., and Ponirakis, D. (**2009**). "Acoustic masking in marine ecosystems: Intuitions, analysis, and implication," Mar. Ecol. Prog. Ser. **395**, 201–222.

Dooling, R. J., and Blumenrath, S. H. (**2014**). "Avian sound perception in noise," in *Animal Communication in Noise*, edited by H. Brumm (Springer Verlag, Heidelberg), pp. 229–250.

Ellison, W. T., Southall, B. L., Clark, C. W., and Frankel, A. S. (**2011**). "A new context-based approach to assess marine mammal behavioral responses to anthropogenic sounds," Conserv. Biol. **26**, 21–28.

Erbe, C. (**2008**). "Critical ratios of beluga whales (*Delphinapterus leucas*) and masked signal duration," J. Acoust. Soc. Am. **124**, 2216–2223.

Erbe, C., Reichmuth, C., Cunningham, K., Lucke, K., and Dooling, R. (**2016**). "Communication masking in marine mammals: A review and research strategy," Mar. Poll. Bull. **103**, 15–38.

Erbe, C., Verma, A., McCauley, R., Gavrilov, A., and Parnum, I. (**2015**). "The marine soundscape of the Perth Canyon," Prog. Oceanogr. **137**, 38–51.

European Commission (**2008**). Maritime Strategy Framework Directive 2008/56/EC, L164/19-40.

Fay, R. R. (**1988**). *Hearing in Vertebrates, A Psychophysics Databook* (Hill-Fay Associates, Winnetka, IL), 621 pp.

Fay, R. R. (**2010**). "Signal-to-noise ratio for source determination and for a co-modulated masker in goldfish, *Carassius auratus*," J. Acoust. Soc. Am. **129**, 3367–3372.

Finneran, J. J. (**2008**). "Modified variance ratio for objective detection of transient evoked potentials in bottlenose dolphins (*Tursiops truncatus*)," J. Acoust. Soc. Am. **124**, 4069–4082.

Finneran, J. J., and Houser, D. S. (**2006**). "Comparison of in air evoked potentials and underwater behavioral hearing thresholds in four bottlenose dolphins," J. Acoust. Soc. Am. **119**, 3181–3192.

Finneran, J. J., and Jenkins, A. K. (**2012**). "Criteria and thresholds for U.S. Navy acoustic and explosive effects analysis," Technical Report, SPAWAR Systems Center Pacific, San Diego, CA, 60 pp.

Harris, G. G. in discussion of Parvulescu, A. (**1967**). "The acoustics of small tanks," in *Marine Bio-Acoustics*, Vol. 2, edited by W. N. Tavolga (Pergamon Press, Oxford), pp. 7–13.

Hawkins, A. D., and Chapman, C. J. (**1975**). "Masked auditory thresholds in the cod, *Gadus morhua* L," J. Comp. Physiol. A. **103**, 209–226.

Hawkins, A. D., Pembroke, A., and Popper, A. N. (**2015**). "Information gaps in understanding the effects of noise on fishes and invertebrates," Rev. Fish. Biol. Fisher. **25**, 39–64.

Hawkins, A. D., Roberts, L., and Cheesman, S. (**2014**). "Responses of free-living coastal pelagic fish to impulsive sounds," J. Acoust. Soc. Am. **135**, 3101–3116.

Houser, D. S., and Finneran, J. J. (**2006**). "Variation in the hearing sensitivity of a dolphin population obtained through the use of evoked potential audiometry," J. Acoust. Soc. Am. **120**, 4090–4099.

Houser, D. S., Gomez-Rubio, A., and Finneran, J. J. (**2008**). "Evoked potential audiometry of 13 Pacific bottlenose dolphins (*Tursiops truncatus gilli*)," Mar. Mammal Sci. **24**, 28–41.

Johnson, C. S. (**1968**). "Masked tonal thresholds in a bottlenose porpoise," J. Acoust. Soc. Am. **44**, 965–967.

Johnson, C. S., McManus, M. W., and Skaar, D. (**1989**). "Masked tonal hearing thresholds in the beluga whale," J. Acoust. Soc. Am. **85**, 2651–2654.

Kastelein, R. A., Hoek, L., de Jong, C. A. F., and Wensveen, P. J. (**2010**). "Effect of signal duration on underwater detection thresholds of a harbor porpoise (*Phocoena phocoena*) for single-frequency-modulated tonal signals between 0.25 and 160 kHz," J. Acoust. Soc. Am. **128**, 3211–3222.

Kastelein, R. A., Wensveen, P. J., Hoek, L., Au, W. W. L., Terhune, J. M., and de Jong, C. A. F. (**2009**). "Critical ratios in harbour porpoises (*Phocoena phocoena*) for tonal signals between 0.315 and 150 kHz in random Gaussian white noise," J. Acoust. Soc. Am. **126**, 1588–1597.

Keith, E. O. (**2008**). "Critical review of the literature on marine mammal population modelling," Report prepared by Nova Southeastern University for E&P Sound & Marine Life Program, 63 pp.

Ketten, D. (**2000**). "Cetacean ears," in *Hearing by Whales and Dolphins*, edited by W. W. L. Au, A. N. Popper, and R. R. Fay (Springer, New York), pp. 43–108.

Kidd, J., Jr., Mason, C. R., Richards, V. M., Gallun, F. J., and Durlach, N. I. (**2008**). "Informational masking," in *Auditory Perception of Sound Sources*, edited by W. A. Yost, A. N. Popper, and R. R. Fay (Springer Science+Business Media, New York), pp. 143–189.

King, S. L., Schick, R. S., Donovan, C., Booth, C. G., Burgman, M., Thomas, L., and Harwood, J. (**2015**). "An interim framework for assessing the population consequences of disturbance," Meth. Ecol. Evol. **6**, 1150–1158.

Ladich, F., and Fay, R. R. (**2013**). "Auditory evoked potential audiometry in fish," Rev. Fish Biol. Fish. **23**, 317–364.

Mooney, T. A., Hanlon, R. T., Christensen-Dalsgaard, J., Madsen, P. T., Ketten, D. R., and Nachtigall, P. E. (**2010**). "Sound detection by the longfin squid (*Loligo pealeii*) studied with auditory evoked potentials: Sensitivity to low-frequency particle motion and not pressure," J. Exp. Biol. **213**, 3748–3759.

Muir, J. E., Gilders, M., and Bychkov, Y. (**2010**). "A conceptual framework for tiered risk assessment to evaluate the effects of sound from E&P operations on marine mammals," Report prepared by LGL Ltd. for E&P Sound & Marine Life Program, 112 pp.

Nachtigall, P. E., Mooney, T. A., Taylor, K. A., Miller, L. A., Rasmussen, M. H., Akamatsu, T., Teilmann, J., Linnenschmidt, M., and Vikingsson, G. A. (**2008**). "Shipboard measurements of the hearing of the white-beaked dolphin *Lagenorhynchus albirostris*," J. Exp. Biol. **211**, 642–647.

National Research Council (**2005**). *Marine Mammal Populations and Ocean Noise: Determining When Noise Causes Biologically Significant Effects* (The National Academy Press, Washington, DC), 126 pp.

Nowacek, D. P., Thorne, L. H., Johnston, D. W., and Tyack, P. L. (**2007**). "Responses of cetaceans to anthropogenic noise," Mamm. Rev. **37**, 81–115.
Pacini, A. F., Nachtigall, P. E., and Quintos, C. T. (**2011**). "Audiogram of a stranded Blainville's beaked whale (*Mesoplodon densirostris*) measured using auditory evoked potentials," J. Exp. Biol. **214**, 2409–2415.
Partan, S. R. (**2013**). "Ten unanswered questions in multimodal communication," Behav. Ecol. Sociobiol **67**, 1523–1539.
Patrick, W. S., Spencer, P., Link, J., Cope, J., Field, J., Kobayashi, D., Lawson, P., Gedamke, T., Cortéz, E., Ormseth, O., Bigelow, K., and Overholtz, W. (**2010**). "Using productivity and susceptibility indices to assess the vulnerability of United States fish stocks to overfishing," Fish. Bull. **108**, 305–322.
Perrin, W. F., Würsig, B., and Thewissen, J. G. M. (**2009**). *Encyclopedia of Marine Mammals* (Academic Press, Amsterdam), 1316 pp.
Pfister, C. A., Esbaugh, A., Frieder, C., Baumann, H., Bockmon, E., White, M., Carter, B., Benway, H., Blanchette, C., Carrington, E., McClintock, J., McCorkle, D., McGillis, J., Mooney, T. A., and Ziveri, P. (**2014**). "Detecting the unexpected: A research framework for ocean acidification," Environ. Sci. Technol. **48**, 9982–9994.
Popper, A. N., and Fay, R. R. (**2011**). "Rethinking sound detection by fishes," Hear. Res. **273**, 25–36.
Popper, A. N., Fay, R. R., Platt, C., and Sand, O. (**2003**). "Sound detection mechanisms and capabilities of teleost fishes," in *Sensory Processing in Aquatic Environments*, edited by S. P. Collin and N. J. Marshall (Springer-Verlag, New York), pp. 3–38.
Popper, A. N., and Hawkins, A. D. (**2016**). *The Effects of Noise on Aquatic Life II* (Springer Science + Business Media, New York), 1224 pp.
Popper, A. N., Hawkins, A. D., Fay, R. R., Mann, D., Bartol, S., Carlson, T., Coombs, S., Ellison, W. T., Gentry, R., Halvorsen, M. B., Løkkeborg, S., Rogers, P., Southall, B. L., Zeddies, D., and Tavolga, W. N. (**2014**). "Sound exposure guidelines for fishes and sea Turtles: A technical report prepared by ANSI-Accredited Standards Committee S3/SC1 and registered with ANSI," ASA S3/SC1.4 TR-2014 (Springer and ASA Press, Cham), 73 pp.
Reichmuth, C., Holt, M. M., Mulsow, J., Sills, J. M., and Southall, B. (**2013**). "Comparative assessment of amphibious hearing in pinnipeds," J. Comp. Physiol. A. **199**, 491–507.
Reuter, H., Breckling, B., and Jopp, F. (**2011**). "Individual-based models," in *Modelling Complex Ecological Dynamics*, edited by F. Jopp, H. Reuter, and B. Breckling (Springer, Heidelberg), Chap. 12, pp. 163–178.
Rogers, P. H., Hawkins, A. D., Popper, A. N., Fay, R. R., and Gray, M. D. (**2016**). "Parvulescu revisited: Small tank acoustics for bioacousticians," in *The Effects of Noise on Aquatic Life II*, edited by A. N. Popper and A. D. Hawkins (Springer Science + Business Media, New York), pp. 933–941.
Samson, J. E., Mooney, T. A., Gussekloo, S. W. S., and Hanlon, R. T. (**2014**). "Graded behavioral responses and habituation to sound in the common cuttlefish *Sepia officinalis*," J. Exp. Biol. **217**, 4347–4355.
Schipper, J., Chanson, J. S., Chiozza, F., Cox, N. A., Hoffmann, M., Katariya, V., Lamoreux, J., Rodrigues, A. S. L., Stuart, S. N., Temple, H. J., Baillie, J., Boitani, L., Lacher, T. E., Mittermeier, R. A., Smith, A. T., Absolon, D., Aguiar, J. M., Amori, G., Bakkour, N., Baldi, R., Berridge, R. J., Bielby, J., Black, P. A., Blanc, J. J., Brooks, T. M., Burton, J. A., Butynski, T. M., Catullo, G., Chapman, R., Cokeliss, Z., Collen, B., Conroy, J., Cooke, J. G., da Fonseca, G. A. B., Derocher, A. E., Dublin, H. T., Duckworth, J. W., Emmons, L., Emslie, R. H., Festa-Bianchet, M., Foster, M., Foster, S., Garshelis, D. L., Gates, C., Gimenez-Dixon, M., Gonzalez, S., Gonzalez-Maya, J. F., Good, T. C., Hammerson, G., Hammond, P. S., Happold, D., Happold, M., Hare, J., Harris, R. B., Hawkins, C. E., Haywood, M., Heaney, L. R., Hedges, S., Helgen, K. M., Hilton-Taylor, C., Hussain, S. A., Ishii, N., Jefferson, T. A., Jenkins, R. K. B., Johnston, C. H., Keith, M., Kingdon, J., Knox, D. H., Kovacs, K. M., Langhammer, P., Leus, K., Lewison, R., Lichtenstein, G., Lowry, L. F., Macavoy, Z., Mace, G. M., Mallon, D. P., Masi, M., McKnight, M. W., Medellin, R. A., Medici, P., Mills, G., Moehlman, P. D., Molur, S., Mora, A., Nowell, K., Oates, J. F., Olech, W., Oliver, W. R. L., Oprea, M., Patterson, B. D., Perrin, W. F., Polidoro, B. A., Pollock, C., Powel, A., Protas, Y., Racey, P., Ragle, J., Ramani, P., Rathbun, G., Reeves, R. R., Reilly, S. B., Reynolds, J. E., Rondinini, C., Rosell-Ambal, R. G., Rulli, M., Rylands, A. B., Savini, S., Schank, C. J., Sechrest, W., Self-Sullivan, C., Shoemaker, A., Sillero-Zubiri, C., De Silva, N., Smith, D. E., Srinivasulu, C., Stephenson, P. J. van Strien, N. Talukdar, B. K., Taylor, B. L., Timmins, R., Tirira, D. G., Tognelli, M. F., Tsytsulina, K., Veiga, L. M., Vie, J.-C., Williamson, E. A., Wyatt, S. A., Xie, Y., and Young, B. E. (**2008**). "The status of the world's land and marine mammals: Diversity, threat, and knowledge," Science **322**, 225–230.
Sisneros, J. A., Popper, A. N., Hawkins, A. D., and Fay, R. R. (**2016**). "Auditory evoked potential audiograms compared to behavioral audiograms in aquatic animals," in *The Effects of Noise on Aquatic Life II*, edited by A. N. Popper and A. D. Hawkins (Springer Science + Business Media, New York), 1224 pp.
Slabbekoorn, H., Bouton, N., van Opzeeland, I., Coers, A., ten Cate, C., and Popper, A. N. (**2010**). "A noisy spring: The impact of globally rising underwater sound levels on fish," Trends Ecol. Evol. **25**, 419–427.
Southall, B. L., Bowles, A. E., Ellison, W. T., Finneran, J. J., Gentry, R. L., Greene, C. R., Jr., Kastak, D., Ketten, D. R., Miller, J. H., Nachtigall, P. E., Richardson, W. J., Thomas, J. A., and Tyack, P. L. (**2007**). "Marine mammal noise exposure criteria: Initial scientific recommendations," Aquat. Mamm. **33**, 411–521.
Southall, B. L., Schusterman, R. J., and Kastak, D. (**2003**). "Auditory masking in three pinnipeds: Aerial critical ratios and direct critical bandwidth measurements," J. Acoust. Soc. Am. **114**, 1660–1666.
Stansbury, A. L., Götz, T., Deecke, V. B., and Janik, V. M. (**2014**). "Grey seals use anthropogenic signals from acoustic tags to locate fish: Evidence from a simulated foraging task," Proc. R. Soc. B **282**, 20141595.
Sun, J. W. C., and Narins, P. (**2005**). "Anthropogenic sounds differentially affect amphibian call rate," Biol. Conserv. **121**, 419–427.
Trickey, J. S., Branstetter, B. B., and Finneran, J. J. (**2011**). "Auditory masking of a 10 kHz tone with environmental, comodulated, and Gaussian noise in bottlenose dolphins (*Tursiops truncatus*)," J. Acoust. Soc. Am. **128**, 3799–3804.
Turnbull, S. D., and Terhune, J. M. (**1990**). "White noise and pure tone masking of pure tone thresholds of a harbour seal listening in air and underwater," Can. J. Zool. **68**, 2090–2097.
Tyack, P. L. (**2008**). "Implications for marine mammals of large-scale changes in the marine acoustic environment," J. Mammal. **89**, 549–558.
Williams, R., Ashe, E., Blight, L., Jasny, M., and Nowlan, L. (**2014**). "Marine mammals and ocean noise: Future directions and information needs with respect to science, policy and law in Canada," Mar. Poll. Bull. **86**, 29–38.
Yost, W. A. (**2013**). *Fundamentals of Hearing*, 5th ed. (Academic Press, San Diego, CA), 352 pp.